

# Dimorphism and endemism in *Hebetoxyites* (Ammonoidea, lower Bajocian) from the Iberian Range (Spain)

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## Abstract

New findings of lower Bajocian, haploceratid ammonites (Cephalopoda, Mollusca) of the genus *Hebetoxyites* from the Albarracín area are described and revised alongside specimens previously collected from the Iberian Range. Three species have been identified: *H. hebes* BUCKMAN, *H. incongruens* BUCKMAN and *H. mousterdei* FERNÁNDEZ-LÓPEZ. Indigenous populations of these Tethyan species in the Iberian carbonate platform system, including macroconchs and microconchs, are interpreted as immigration and colonization of shallow-water marine environments by Submediterranean taxa during a short interval of the early Bajocian. As peramorphic result of palingenetic evolution, a chronocline from strongly ribbed, stout forms of the Ovale Zone (including *H. mousterdei*), to oxycones with blunt, simple or irregularly branched ribbing of the Laeviuscula Zone (including *H. incongruens*), through intermediate forms belonging to *H. hebes*, has been recognized. These successive species of *Hebetoxyites* provide a basis for correlation and subzonal division of the Ovale and Laeviuscula zones in the Iberian Range.

## Keywords

Ammonites, Middle Jurassic, Taphonomy, Systematics, Evolution, Submediterranean Province.

## Resumen

**Dimorfismo y endemismo en *Hebetoxyites* (Ammonoidea, Bajociense inferior) de la Cordillera Ibérica.** Nuevos ammonites haplocerátidos (Cephalopoda, Mollusca) del Bajociense inferior del género *Hebetoxyites* hallados en el área de Albarracín son descritos junto a ejemplares revisados de colecciones previas de la Cordillera Ibérica. Tres especies han sido identificadas: *H. hebes* BUCKMAN, *H. incongruens* BUCKMAN y *H. mousterdei* FERNÁNDEZ-LÓPEZ. Las poblaciones indígenas de estas especies del Tethys en el sistema de plataformas carbonáticas de Iberia, incluyendo macroconchas y microconchas, son interpretadas como un resultado de inmigración y colonización de ambientes marinos poco profundos, por taxones submediterráneos durante un breve intervalo del Bajociense temprano. Como resultado peramórfico de evolución palingenética, una cronocline ha sido reconocida: desde formas robustas, fuertemente costuladas, de la Zona Ovale (pertenecientes a *H. mousterdei*), hasta oxiconos de costulación roma, simple o irregularmente ramificada, con numerosas secundarias en el flanco externo de la Zona Laeviuscula (incluyendo *H. incongruens*), pasando por formas intermedias pertenecientes a *H. hebes*. Estas especies sucesivas de *Hebetoxyites* permiten establecer una división y correlación subzonal de las zonas Ovale y Laeviuscula en la Cordillera Ibérica.

## Palabras claves

Ammonites, Jurásico Medio, Tafonomía, Sistemática, Evolución, Provincia Submediterránea.

## I. INTRODUCTION

*Hebetoxyites* are mainly known from Tethyan areas, as a relatively scarce component of certain lower Bajocian ammonite assemblages (BUCKMAN 1922, 1924, in 1909-1930; FERNÁNDEZ-LÓPEZ, 1985, 2011; SANDOVAL, 1985; BENSHILI, 1989, 1990; SADKI, 1996; DIETZE *et al.*, 2007; YIN, 2010). In addition, *Hebetoxyites* from north-eastern Pacific areas have also been figured (WESTERMANN, 1969, 1992; IMLAY, 1973, 1984; TAYLOR, 1988; POULTON *et al.*, 1992). *Hebetoxyites* are relatively scarce, less than 5%, in the Iberian Range and the Catalan Coastal Range (Fig. 1). New field samplings in the Albarracín area and the revision of earlier collections provided more than one hundred macroconchs and microconchs of this

genus, collected bed by bed, from the Ovale and Laeviuscula zones.

The primary aim is to focus on the significance and diversity of *Hebetoxyites* at the Iberian carbonate platform system, from a taphonomic and palaeobiological view point, and identify its palaeobiogeographical and biochronological relevance.

## II. PALAEOENVIRONMENTAL AND PALAEO-BIOGEOGRAPHICAL SETTING

Aalenian and lowermost Bajocian deposits of the Iberian Range are commonly represented by condensed sections with stratigraphical discontinuities (GÓMEZ &

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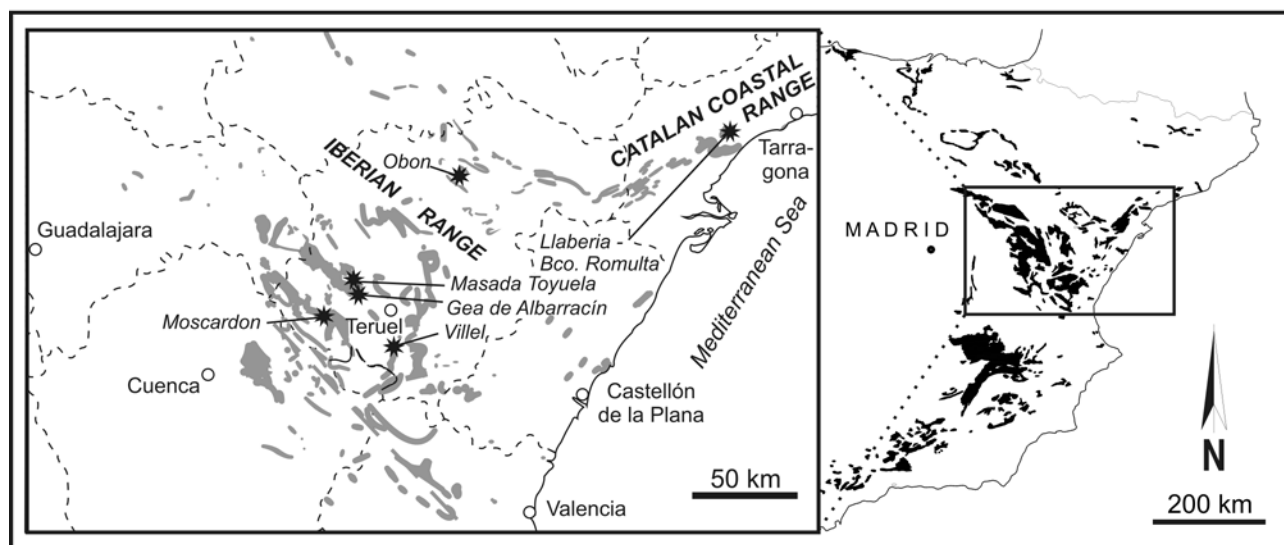


Fig. 1: Location maps. Asterisks indicate the stratigraphical sections cited in text. Black areas represent outcrops of Jurassic deposits, with gray areas representing outcrops of Middle Jurassic deposits in the Iberian Range and the Catalan Coastal Range (Spain). Dashed lines indicate the province boundaries.

FERNÁNDEZ-LÓPEZ, 2006). Taphonomic analysis of ammonite fossil-assemblages and taphofacies provide significant information on palaeoenvironmental cycles developed in the open-marine, carbonate deposits of the External Castilian, Aragonese and Tortosa platforms (FERNÁNDEZ-LÓPEZ & GÓMEZ, 2004), independently tested with data of sequence stratigraphy. Particularly, taphonomic information of the lowermost Bajocian ammonite assemblages include the abundance of reelaborated, heterogeneous concretionary internal moulds, isolated concretionary body chambers and hollow ammonites, bearing traces of abrasion, bioerosion and encrusting organisms. These palaeoenvironmental indicators imply low rates of sedimentation, punctuated by occasional high rates of sediment accumulation, due to sedimentary winnowing and bypassing interrupted by storm deposition in shallow-water marine environments (FERNÁNDEZ-LÓPEZ, 2011). These taphonomic results corroborate the development of an incipient-deepening phase, which represents the first episode of a deepening half-cycle of third order, in the Castilian Platform during the Bajocian, Ovale and Laeviuscula biochrons (FERNÁNDEZ-LÓPEZ, 1997, 2004, 2011).

In the Iberian platform system, the distribution of ammonite shells was taphonomically and ecologically controlled by regional changes of relative sea level. Generally, early Bajocian ammonite assemblages of the Castilian Platform show a mixing of NW European and Mediterranean elements with some Submediterranean representatives. Ammonite shell supply occurred preferentially from more septentrional epicontinental seas; however, the proportion of Mediterranean elements increased during the early Bajocian.

Macroconchs and microconchs of ammonites represent distinct taphonomic groups, or taphons, due to their structural and behaviour differences (FERNÁNDEZ-LÓPEZ, 2006, 2007). Taphons are integrated by local taphonic populations, which can be preserved in particular environments. Within early Bajocian ammonite assemblages of the Castilian Platform, taphonic populations of type-3 dominate, whereas type-2 is very scarce and 1 is virtually absent. Type-3 populations have unimodal or polymodal, asymmetric distribution of size frequencies, with negative skew and dominant adults, juvenile shells are virtually absent. Type-1 populations, dominated by juvenile shells, indicate endemic taxa. Generally, autochthonous biogenic production of shells is not recognized. Most early Bajocian ammonites of the Castilian Platform, dominated by adults are the result of regional necrokinosis or local immigration without sustained colonization. Most of these lower Bajocian ammonite shells of the Castilian Platform represent ademic organisms interpreted as allochthonous elements arriving at their present location by necroplanktic drift from northern, more open marine or oceanic areas. In contrast, some genera including *Hebetoxites* (Fig. 2) show taphonic populations of type-2, comprising monospecific or polyspecific shells with unimodal, normal distribution of size-frequencies with dominant pre-adults and absence of juveniles. Microconchs occur in low proportions. Several fragmentary *Hebetoxites* macroconchs from the Iberian Range indicate adult-sizes larger than 200 mm, although *H. hebes*, *H. incongruens* and *H. mouterdei* have adult-sizes larger than 95, 85 and 80 mm respectively. The occurrence of type-2 populations without evidence of sorting by necroplanktic drift or transport indicates autochthonous biogenic pro-

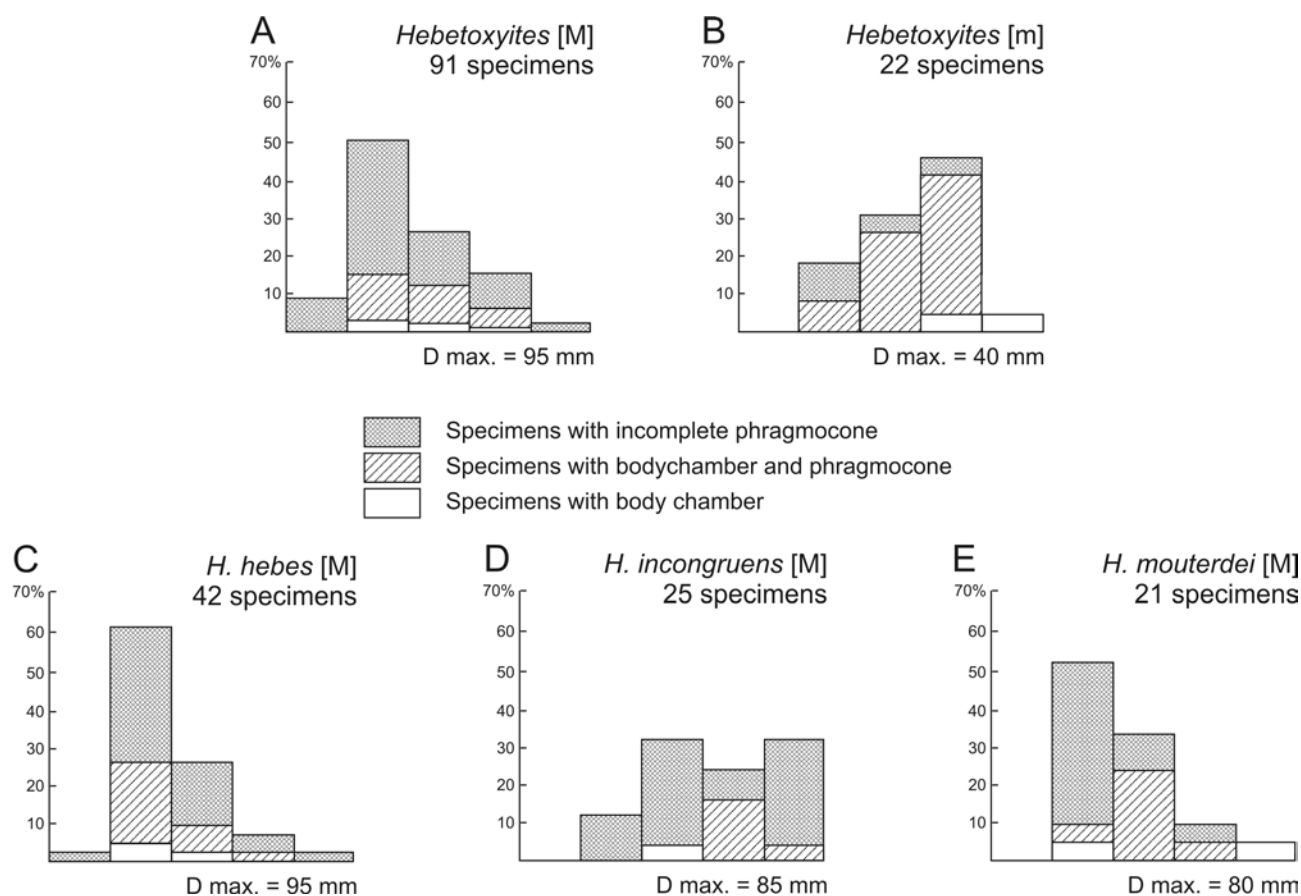


Fig. 2: Size-frequency distributions of macroconchs (A) and microconchs (B) of *Hebetoxyites* from the Iberian Range, including macroconchs of *Hebetoxyites hebes* (C), *H. incongruens* (D) and *H. mouterdei* (E). The histograms of taphonic populations are plotted in terms of five frequency classes, indicating the proportion of bodychambers, complete shells (with bodychamber and phragmocone) and incomplete phragmocones. Note the higher relative abundance of bodychambers in the intermediate classes or frequency groups, as diagnostic criterion of taphonic populations of type-2.

duction of shells by miademic (actively biodispersed) or parademic (passively biodispersed), indigenous populations of *Hebetoxyites* on the Iberian platform system. Immigration and colonization of the eastern margin of Iberia by demic *Hebetoxyites* in the Ovale and Laeviuscula zones is evidence of a deepening episode, but these habitats were epicontinental platforms with neritic environments flooded by shallow marine waters.

*Hebetoxyites* seems pandemic, but species of *Hebetoxyites* from the Iberian Range (*H. hebes*, *H. incongruens* and *H. mouterdei*) are notably western Tethyan in distribution. The occurrence of populations inhabiting shallow-water marine environments of the Iberian platform system is interpreted as being diagnostic criterion of the Submediterranean endemic nature of these three early Bajocian species.

### III. SYSTEMATICS

**Class Cephalopoda CUVIER, 1798**  
**Subclass Ammonoidea ZITTEL, 1884**

**Order Ammonitida ZITTEL, 1884**  
**Suborder Haplocerina BESNOSOV & MICHAILOVA, 1983**  
**Superfamily Haploceratoidea ZITTEL, 1884**  
**Family Hebetoxyitidae BUCKMAN, 1924**

BUCKMAN (1924 in 1909-1930) erected the family Hebetoxyitidae to include *Hebetoxyites*, *Kleistoxyites* and *Amblyoxyites*. They have discoidal shells, which lack a keel, with rounded venter, falcoid ribs and moderately complex sutures. The rounded venter and suture-line are of lissoceratid style. In *Hebetoxyites* it is less complex than in *Lissoceras*, but in *Amblyoxyites* it attains almost the complexity of an oppelid. In Hebetoxyitidae, the ribs continue across the whorl, whereas in oppelids ribbing is irregular with primary ribs divided by secondaries which are often confined to the outer part of the flank. BUCKMAN (1924 in 1909-1930) considered the phyletic position of the Hebetoxyitidae to be after the Lissoceratidae, with an origin similar to oppelids.

The Hebetoxyitidae, in particular *Hebetoxyites*, differ from Strigoceratidae by the absence of hollow floored

keel, strigation and a simpler suture line characteristic of the Oppeliidae (ARKELL, 1950; STURANI, 1971; TAYLOR, 1988; DIETZE *et al.*, 2007; SCHWEIGERT *et al.*, 2007). *Hebetoxyites* has been placed in the Strigoceratidae due to its falcoid or falcate ribbing and lateral spiral ridge (ARKELL *et al.*, 1957; SCHINDEWOLF, 1963 in 1961-1968; IMLAY, 1964, 1973, 1984; WESTERMANN, 1969; CALLOMON, 1981; PAVIA, 1983; FERNÁNDEZ-LÓPEZ, 1985; SANDOVAL, 1985, 1990; CALLOMON & CHANDLER, 1990; CECICA *et al.*, 1991; SADKI, 1996; RIOULT *et al.*, 1997; YIN, 2010). CALLOMON (1981) included the Hebetoxyitidae as a synonym of Strigoceratidae, but erected a new subfamily Bradfordiinae, separating the Oppeliinae sensu stricto to make two distinct phyletic strands of the Oppeliidae based, respectively, in *Bradfordia* and *Oppelia*. DIETZE *et al.* (2007) considered *Amblyoxyites* BUCKMAN, *Toxamblyites* BUCKMAN, *Stegoxyites* BUCKMAN and perhaps *Hebetoxyites* BUCKMAN to fall somewhere between these two phyletic strands, lacking strigation and a hollow floored keel characteristic of strigoceratids. *Hebetoxyites* was excluded from the Strigoceratidae and included in the Oppeliidae *s.l.* WESTERMANN (1969) and FERNÁNDEZ-LÓPEZ (1985) concluded that the microconchs of *Hebetoxyites* were minute, evolute and with lateral lappets. The larger macroconchs are involute with simple peristome. This hypothesis is examined further here. The earliest known Hebetoxyitidae occur in the Aalenian, Concavum Zone of north-eastern Pacific areas (TAYLOR, 1988; POULTON *et al.*, 1992) and the latest representatives have been referred to the Humphriesianum Zone of Tibet (YIN, 2010). The phyletic position of the monospecific genus *Kleistoxyites* from the Discites Zone of England (BUCKMAN, 1922 in 1909-1930, pl. 317; CALLOMON & CHANDLER, 1990) needs further investigation. The Hebetoxyitidae, based in *Hebetoxyites*, show inner whorls smooth with rounded venter, such as in *Lisuoceras* and *Amblyoxyites*, but ribbing not projected at the venter and the intermediate and outer whorls display blunt fastigation. Therefore, within the superfamily Haploceratoidea (ZITTEL, 1884) of the suborder Haplocerina (BESNOSOV & MICHAILOVA, 1983; cf. SHEVYREV, 2006; PAGE, 2008), besides the basal families Lissoceratidae (DOUVILLE, 1885) and Oppeliidae (DOUVILLE, 1890), the family Hebetoxyitidae (BUCKMAN, 1924 in 1909-1930) evolved during the late Aalenian and early Bajocian.

#### Genus *Hebetoxyites* BUCKMAN, 1924

**Type species:** *Hebetoxyites hebes* BUCKMAN, 1924 in 1909-1930, by original designation (BUCKMAN, 1924 in 1909-1930, pl. 475).

**Diagnosis:** Discoidal shells from small to medium size. Shells are compressed to oxycones, with a slight rise of the flanks around two-fifths of the whorl height. The umbilicus is narrow ( $U/D = 5\text{--}35\%$  in post-juvenile stages; Fig. 3), with distinct or raised margin. The whorl section

- △ ▲ *Hebetoxyites hebes* Buckman [M+m]  
 □ ■ *Hebetoxyites incongruens* Buckman [M+m]  
 ○ ● *Hebetoxyites mouterdei* Fernandez-Lopez [M+m]

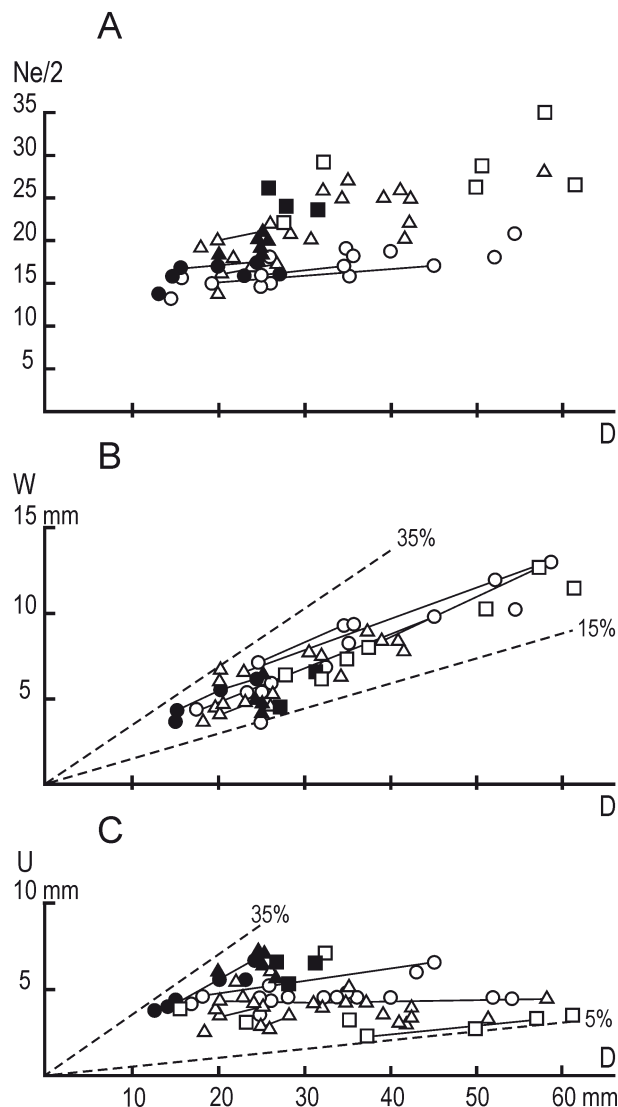


Fig. 3: Plots of measurements of *Hebetoxyites* from the Iberian Range. A, external ribs per half whorl ( $Ne/2$ ) versus shell diameter ( $D$ ). B, whorl-width ( $W$ ) versus shell diameter ( $D$ ). C, umbilical diameter ( $U$ ) versus shell diameter ( $D$ ).

is broadest at the lateral ridge, from which ventrally the flanks converge gently towards a narrow rounded venter. The inner whorls are smooth, with a rounded venter. Mid and outer whorls have a blunt fastigate venter, but never a keel. The aperture is simple in macroconchs and possesses lappets in microconchs.

Ribbing is falcoid or falcate, with blunt costae, simple or irregularly branched which may become stronger on the outer half of the flank. Primaries are bundled at the inner flank. The ribbing abuts the venter but is not projected



forward at the periphery and weakens on the outer flank through ontogeny. On the adult body chamber the ribbing fades completely or is very feeble. The suture line is moderately complex. The ventral lobe is wide, with a moderately broad lateral lobe extending beyond the ventral and second lateral lobes. The second lateral saddle is higher than the first lateral saddle (Fig. 4).

**Discussion:** Adult *Hebetoxyites* microconchs have a tendency to develop elliptical coiling of the last whorl, with the body chamber becoming more inflated, the whorl height is reduced while the venter becomes more rounded. Microconchs with lappets have been suggested among specimens from Alaska (WESTERMANN, 1969, 1992) and the Iberian Range (FERNÁNDEZ-LÓPEZ, 1985). However, the Alaskan adult internal moulds with lappets have a more elliptical coiling style than the Iberian specimens, with the umbilical seam egressing almost radially before returning to spiral coiling. The Alaskan microconchs referred to this taxon were associated with macroconchs of “*Bradfordia*? (*Praeoppelia*) *oppeliiformis*” WESTERMANN (1969, p. 48) so the possible dimorphism between these Alaskan microconchs and macroconchs needs further study.

The inner whorls of microconch from the Iberian Range have a rounded venter, similar to *Protoecotraustes* SPATH (1928 in 1927-1933; type species “*P. dundriensis*” SPATH, 1928 in 1927-1933) and *Microliissoceras* STURANI (1971; type species “*Lissoceras* (*Microliissoceras*) *pusillum*” STURANI, 1971). However, *Protoecotraustes* develops a tabulate venter on the outer whorl and *Microliissoceras* lacks a distinct or raised umbilical margin. *Oecotraustes* WAAGEN (1869; type species “*O. genicularis*” WAAGEN, 1869) has a feeble keeled. The ribbing of *Hebetoxyites*

macroconchs has similarities with a number of other published taxa, including: *Oppelia* WAAGEN (1869; type species “*Ammonites subradiatus*” J. DE C. SOWERBY, 1823 in SOWERBY & SOWERBY, 1812-1846), *Strigoceras* QUENSTEDT (1886; type species “*Ammonites truellei*” D’ORBIGNY, 1845 in 1842-50), *Bradfordia* BUCKMAN (1910; type species: “*B. liomphala*” BUCKMAN, 1910, pl. 10, figs. 4-5), *Amblyoxyites* BUCKMAN (1922 in 1909-1930; type species “*A. amblys*” BUCKMAN, 1922 in 1909-1930, TA-IV, pl. 303), *Kleistoxyites* BUCKMAN (1922 in 1909-1930; type species “*K. protrusus*” BUCKMAN, 1922 in 1909-1930, TA-IV, pl. 317), *Liroxyites* IMLAY (1961; type species “*Oppelia* (*Liroxyites*) *kellumi*” IMLAY, 1961), *Praeoppelia* WESTERMANN (1969; type species “*P. oppeliiformis*” WESTERMANN, 1969) or *Etropolia* SAPUNOV (1971; type species “*Harpoceras blumius*” DE GREGORIO, 1886). However, *Oppelia* has a feeble keel and complex sutures, with wide first lateral lobe. *Strigoceras* has strigation on the test, a tall hollow floored keel and complex sutures. *Bradfordia*, *Amblyoxyites*, *Praeoppelia* and *Etropolia* have a rounded venter with ribs projected or forming blunt chevrons. *Kleistoxyites* appears to be older and has more complex sutures, with narrow first lateral lobe and longer ventral lobe. *Liroxyites* IMLAY is younger and show complex sutures.

**Distribution:** *Hebetoxyites* appears to be pandemic, known in both Tethyan and Pacific areas. Tethyan *Hebetoxyites* are known from Europe, northern Africa and Tibet: England (BUCKMAN, 1924 in 1909-1930; PARSONS, 1979; DONOVAN *et al.*, 1981; DIETZE *et al.*, 2007), France (RIOULT *et al.*, 1997), Iberian Basin (FERNÁNDEZ-LÓPEZ, 1985, 2011; FERNÁNDEZ-LÓPEZ *et al.*, 1996, 1999), Apennines (CRESTA & GALACZ, 1990; CECCA *et*

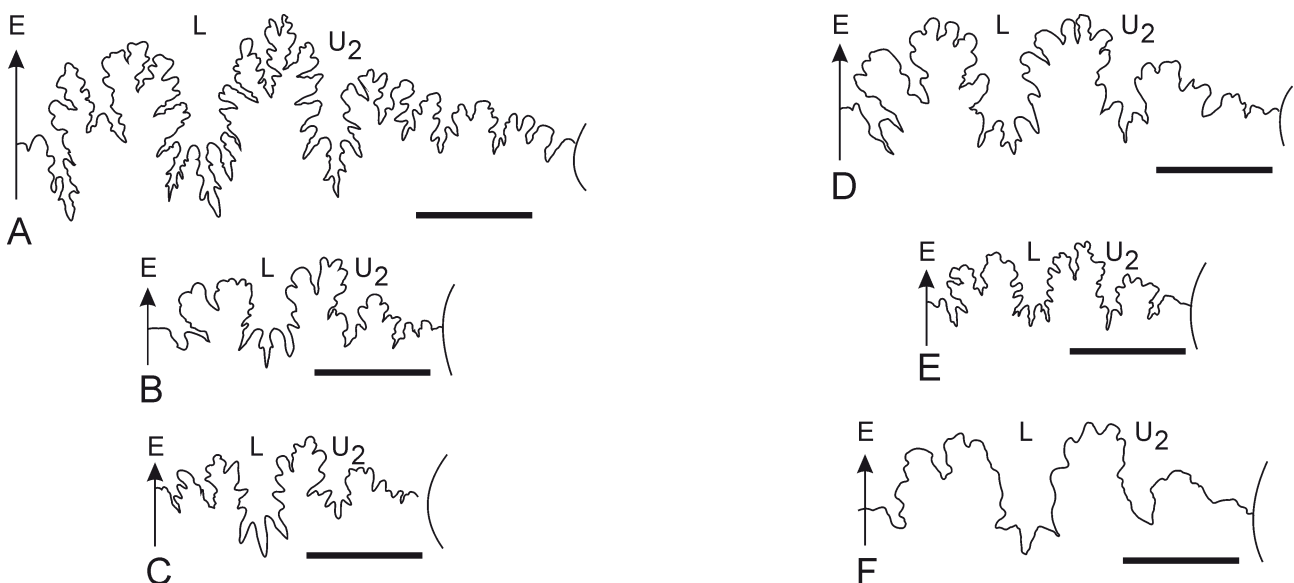


Fig. 4: Suture lines of *Hebetoxyites* from the Iberian Range. Scale bar 1 mm. A, *H. hebes*, macroconch MT2/325. B, *H. hebes*, microconch MT2d/1206. C, *H. hebes*, macroconch MT2/353. D, *H. incongruens*, microconch MT2/366. E, *H. incongruens*, microconch MT2/365. F, *H. mousterdei*, microconch ON17/1.

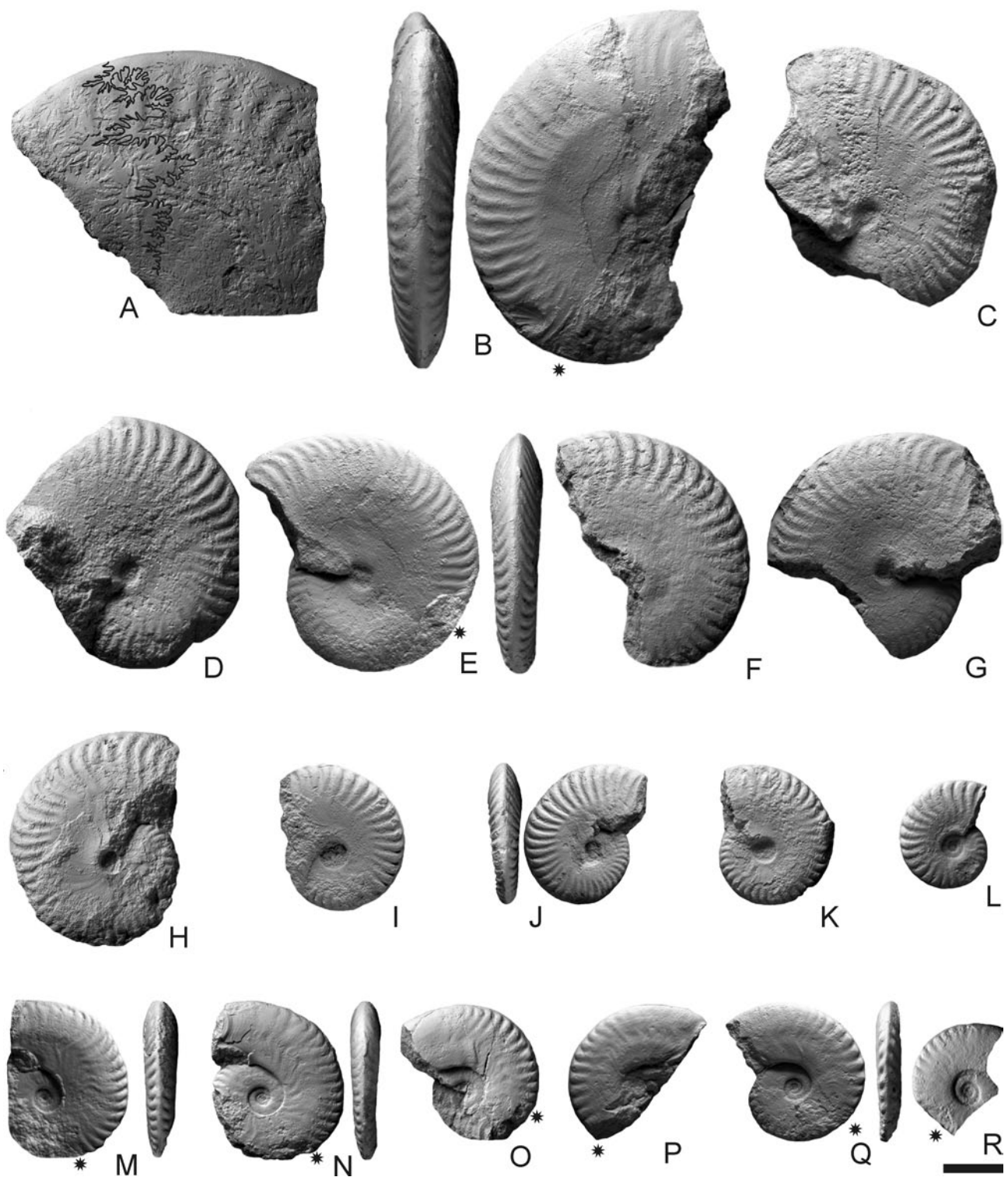


Fig. 5: *Hebetoxyites hebes* BUCKMAN, 1924 in 1909-1930 [M & m]. Ovale and Laeviuscula zones. Black asterisk marks the last septum of the phragmocone. The specimens were whitened with magnesium oxide prior to photography. Scale bar 10 mm. A, macroconch 1MT2/315, left side view of incomplete phragmocone. B, macroconch 1MT2/1, ventral and left side views. C, macroconch 1MT2/321, right side view. D, macroconch 1MT2/329, right side view. E, macroconch 1MT2/358, right and ventral side views. F, macroconch 1MT2/326, right side view. G, macroconch 1MT2/302, left side view. H, macroconch 1MT2/325, left side view. I, macroconch 1MT2/331, right side view. J, macroconch 1MT2/354, ventral and left side views. K, macroconch 2GA21/2, right side view. L, macroconch 1MT2/353, left side view. M, microconch 1MT2/369, right and ventral side views. N, microconch 1MT2/370, right and ventral side views. O, microconch 1MT2/372, right side view. P, microconch 1MT2/367, left side view. Q, microconch 1MT2d/1206, right and ventral side views. R, microconch 1MT2/1205, left side view.

*al.*, 1991; CRESTA *et al.*, 1995), Alps (PAVIA, 1983), Bevic Basin (SANDOVAL, 1985, 1990; JIMÉNEZ *et al.*, 1999; SANDOVAL *et al.*, 2001), Atlas (BENSILIL, 1989, 1990; SADKI, 1996) and Tibet (YIN, 2010). In the Pacific areas it occurs in Alaska (WESTERMANN, 1969, 1992; IMLAY, 1984), Western Canada (POULTON *et al.*, 1992) and Oregon (IMLAY, 1973; TAYLOR, 1988).

***Hebetoxyites hebes* BUCKMAN, 1924 [M & m]  
Figs. 4A-C, 5A-R, Tabl. 1**

1924. *Hebetoxyites hebes* BUCKMAN, 1909-1930, TA-5, pl. 475 (holotype).  
1924. *Hebetoxyites clypeus* BUCKMAN, 1909-1930, TA-5, pl. 496A (holotype)-496B.  
1985. *Hebetoxyites clypeus* BUCKMAN. – FERNÁNDEZ-LÓPEZ, p. 153, pl. 14, fig. 1.

**Material:** 52 specimens from three localities: 2 specimens from Gea de Albarracín (Ovale Zone: 2GA21/2; Laeviuscula Zone: 1GA39/1,) 49 specimens from Masada Toyuela (Laeviuscula Zone: 1MT2/1, 7, 9, 12-13, 302, 314-315, 321, 325-326, 329, 331-338, 341-243, 345, 347-349, 351-355, 358-359, 361, 367, 369, 370-373, 1062-1063; upper Laeviuscula Zone: 1MT2d/1205-1206, 1208; 3MT14/1-2, 4) and 1 specimen from Llaberia-Bco. Romulta (Ovale Zone: 36L6/1).

**Diagnosis:** Macroconch and microconch specimens with a minute or narrow umbilicus and distinct or slightly raised umbilical margin. The inner flanks are slightly convex. Ribbing is falcoid, simple or irregularly branched, with some secondaries on the outer flank.

**Discussion:** Iberian collections of this taxonomic group are dominated by pre-adults along with several fragmentary specimens indicating adult sizes larger than 95 mm. The holotype of *H. hebes*, lacks elliptical coiling of the last whorl and would appear to be a pre-adult of approximately 70 mm diameter. It came from the Lower White Ironshot of Dundry in Avon (England). The syntypes of *H. clypeus* are incomplete phragmocones, from the lower part of the Fossil Bed of Sandford Lane near Sherborne (England; R. CHANDLER *pers. com.*; cf. Buckman, 1893, bed 6d.) and the holotype is a specimen in excess of 200 mm diameter. Specimens of *H. clypeus* and *H. cf. hebes* were identified in the Iberian Range (FERNÁNDEZ-LÓPEZ, 1985) and Catalan coastal Range (FERNÁNDEZ-LÓPEZ *et al.*, 1996, 1999). However, considering their similar morphological features and close parallel chronology, *H. clypeus* is interpreted here as a junior synonym of *H. hebes*. Some specimens from England identified as *H. hebes* (DIETZE *et al.*, 2007, fig. 7e) and others from the Betic Basin identified as *H. incongruens* (SANDOVAL, 1985, pl. 2, figs. 5-9) with prominent costae and a raised umbilical margin, may belong to *H. mouterdei*. Tibetan specimens ascribed to *H. cf. hebes* (YIN, 2010, pl. 5, figs. 5-7) are stout-whorled and probably younger than the West Tethyan examples.

**Distribution:** *H. hebes* is the commonest and most widely distributed species of the genus, characterizing the lower Bajocian, Ovale and Laeviuscula zones of England (BUCKMAN, 1924 in 1909-1930; PARSONS, 1979; DONOVAN *et al.*, 1981; DIETZE *et al.* 2007), Iberian Basin (FERNÁNDEZ-LÓPEZ, 1985, 2011; FERNÁNDEZ-LÓPEZ *et al.*, 1996, 1999), Betic Basin (SANDOVAL, 1990; JIMÉNEZ *et al.*, 1999; SANDOVAL *et al.*, 2001), Atlas (SADKI, 1996) and France (RIOULT *et al.*, 1997).

***Hebetoxyites incongruens* BUCKMAN, 1924 [M & m]  
Figs. 4D-E, 6A-J, Tabl. 2**

1924. *Hebetoxyites incongruens* BUCKMAN, 1909-1930, TA-5, pl.497 (holotype).  
2007. *Hebetoxyites incongruens* BUCKMAN.– SCHWEIGERT *et al.*, p. 49, fig. 27 (holotype).

**Material:** 29 specimens from Masada Toyuela (Laeviuscula Zone: 1MT2/2, 6, 8, 306, 313, 316-318, 320, 322-324, 328, 330, 339, 344, 350, 356, 357, 360, 365, 368; upper Laeviuscula Zone: 1MT2d/366, 1204, 1209-1210, 1212-1214).

**Diagnosis:** Macroconchs and microconchs with a minute or very narrow umbilicus and distinct umbilical margin and inner flank that is flat or slightly convex. The ribbing is falcoid, simple or irregularly branched, with numerous secondaries on the outer flank.

**Discussion:** The Iberian specimens of this taxonomic group are dominated by pre-adults and fragmentary specimens indicating adult-sizes larger than 85 mm diameter. The holotype of *H. incongruens* comes from the Fossil Bed of Sandford Lane. It is an incomplete pre-adult of size larger than 70 mm diameter. The holotype and Iberian specimens differ from *H. hebes* in morphology, by being more involute and possessing numerous secondaries on the outer flank.

**Distribution:** The holotype of *H. incongruens*, from the Fossil Bed of Sandford Lane near Sherborne (England), probably corresponds to the lower Laeviuscula Zone (BUCKMAN, 1924 in 1909-1930; SCHWEIGERT *et al.*, 2007). The species has been collected from the same zone of the Betic Basin (SANDOVAL, 1990) and Atlas (SADKI, 1996). The known specimens from the Iberian Range also correspond to the Laeviuscula Zone.

***Hebetoxyites mouterdei* FERNÁNDEZ-LÓPEZ, 1985  
[M & m]  
Figs. 4F, 7A-L, 8, Tabl. 3**

1985. “*Hebetoxyites*” *mouterdei* FERNÁNDEZ-LÓPEZ, p. 155, figs. 13-14c, pl. 14, fig. 5A-B (holotype).  
1985. *Hebetoxyites* aff. *clypeus* BUCKMAN.– FERNÁNDEZ-LÓPEZ, p. 154, pl. 14, fig. 2A-B.  
1985. *Hebetoxyites incongruens* BUCKMAN.– SANDOVAL, p. 106, pl. 2, figs. 5-9.  
2007. *Hebetoxyites hebes* BUCKMAN.– DIETZE *et al.*, p. 20, fig. 7e.



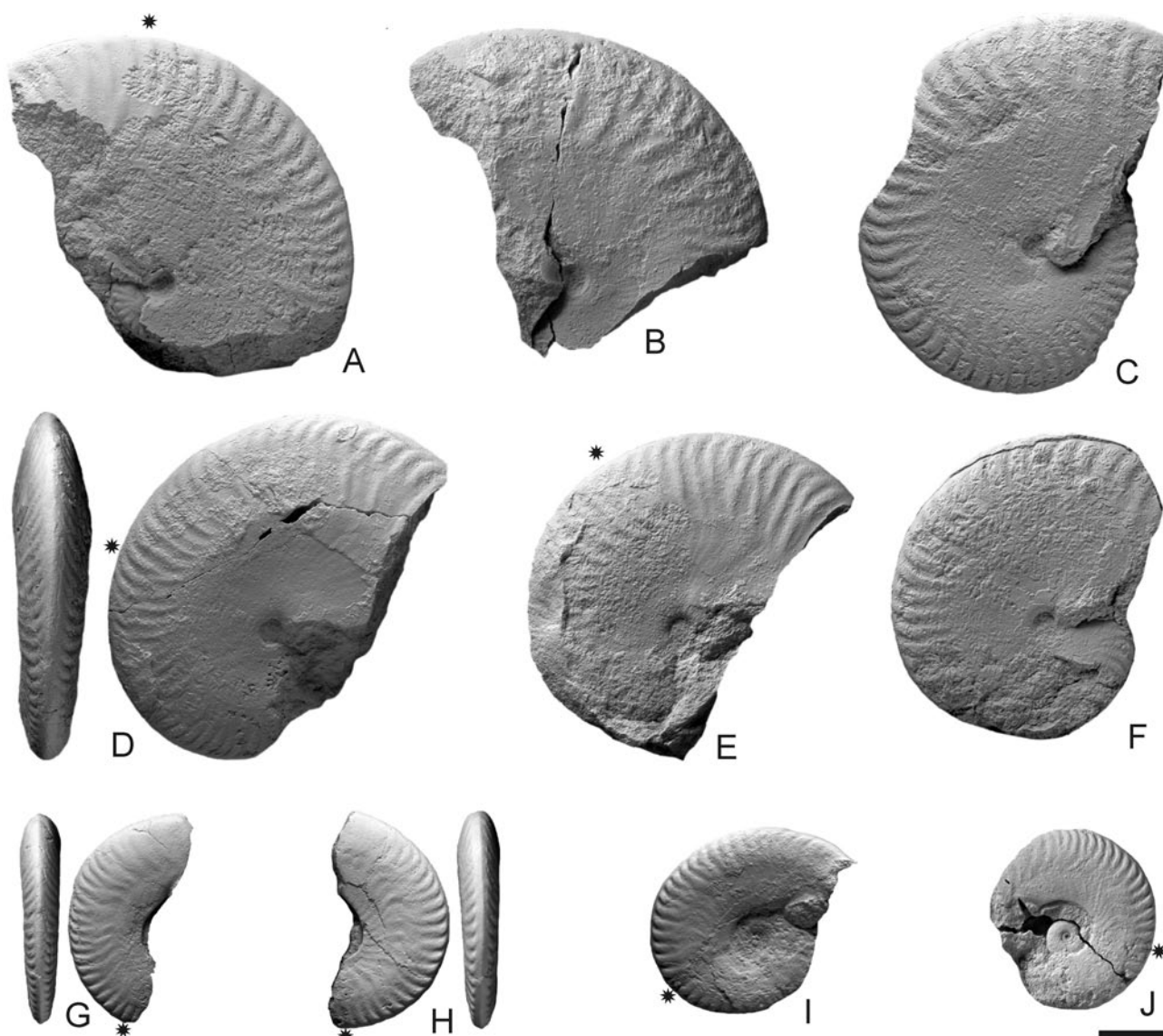


Fig. 6: *Hebetoxyites incongruens* BUCKMAN, 1924 in 1909-1930 [M & m]. Laeviuscula Zone. Scale bar 10 mm. A, macroconch 1MT2/356, right side view. B, macroconch 1MT2/322, right side view. C, macroconch 1MT2/318, left side view. D, macroconch 1MT2d/1212, ventral and left side views. E, macroconch 1MT2/2, left side view. F, macroconch 1MT2/324, left side view. G, microconch 1MT2d/1204, ventral and left side views. H, microconch 1MT2/368, right and ventral side views. I, microconch 1MT2/366, left side view. J, microconch 1MT2/365, right side view.

**Material:** 27 specimens from five localities: 1 specimen from Gea de Albarracín (Ovale Zone: 2GA21/1); 21 specimens from Masada Toyuela (Ovale Zone: 1MT2a/4-5, 11; Ovale and Laeviuscula zones: 1MT2/301, 303-305, 307-312, 319, 327, 340, 346, 1042, 1049, 1069, 1211); 3 specimens from Moscardon (Ovale and Laeviuscula zones: M10U50/16, M10U75/9, M12L5/5); 1 specimen from Obon (Ovale Zone: ON17/1) and 1 specimen from Villel (Laeviuscula Zone: VE1t/1).

**Diagnosis:** Macroconchs and microconchs. The umbilicus is narrow with a raised margin. The inner flanks are markedly convex abutting the raised umbilical edge with a shallow depression on the most dorsolateral portion of

the flank. The ribbing is falcoid and simple. Costae are prominent and cover the inner and outer areas of the mid flank. They are sometimes bundled in pairs on the inner flank area.

**Discussion:** The holotype of *H. mouterdei* (Figs. 7L and 8) is an incomplete specimen of a pre-adult, probably a microconch, greater than 25 mm diameter. Among the Iberian macroconchs of this taxonomic group, pre-adults are dominant and several fragmentary specimens indicate adult-sizes larger than 80 mm diameter. The Iberian specimens differ from *H. hebes* and *H. incongruens* morphologically in being less compressed, more evolute, with a raised umbilical margin and more prominent



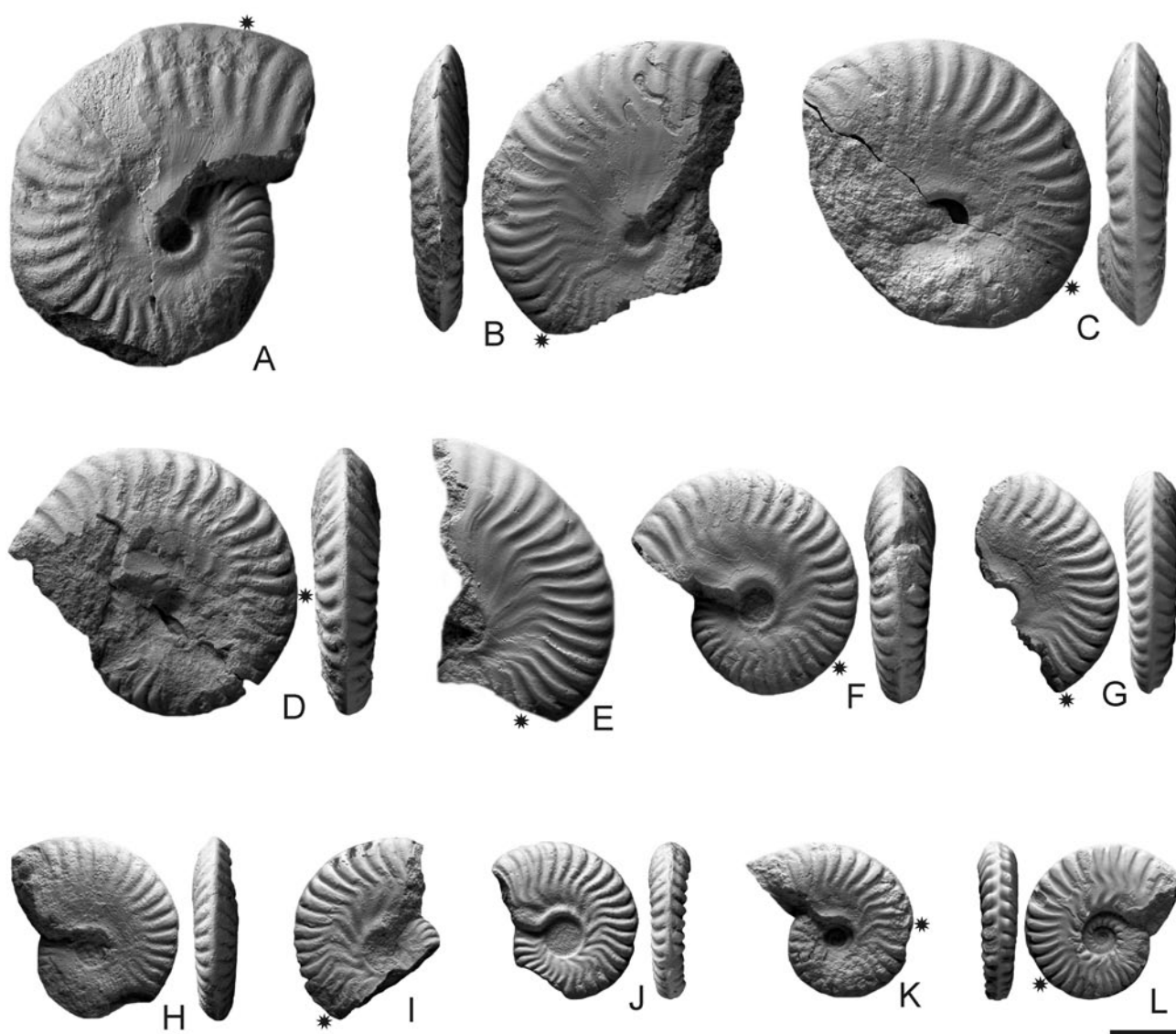


Fig. 7: *Hebetoxyites mouterdei* FERNÁNDEZ-LÓPEZ, 1985 [M & m]. Ovale and Laeviuscula zones. Scale bar 10 mm. A, macroconch 1MT2/310, left side view. B, macroconch 1MT2/4, ventral and left side views. C, macroconch 1MT2/5, right and ventral side views. D, macroconch 1MT2/312, right and ventral side views. E, macroconch 1MT2/311, right side view. F, macroconch 1MT2/1211, right and ventral side views. G, macroconch 1MT2/301, right and ventral side views. H, macroconch 1MT2/1049, right and ventral side views. I, macroconch 1MT2/305, left side view. J, macroconch 1MT2/308, right and ventral side views. K, macroconch 1MT2/1069, right side view. L, microconch ON17/1, ventral and left side views of holotype.

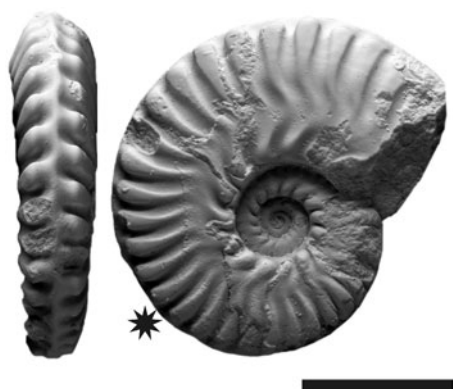


Fig. 8: Holotype of *Hebetoxyites mouterdei* FERNÁNDEZ-LÓPEZ [m]. Ovale Zone from Obon (Teruel). Ventral and left side views, specimen ON17/1. Phosphatic internal mould of bodychamber and phragmocone with local remains of calcitic pseudomorphic shell. Scale bar 10 mm.

costae. *Hebetoxyites snowshoensis* TAYLOR (1988, p. 135, p. 4, figs. 1-2), from the Discites Zone of Oregon has stouter whorls, a broader and more rounded venter and weaker ribbing on the outer flank.

**Distribution:** All the Iberian specimens known of this species are reelaborated elements recorded in deposits of the Laeviuscula Zone. However, at least some of these specimens, including the holotype, probably belong to the Ovale Zone. This species is also identified in Laeviuscula Zone of the Betic Basin (SANDOVAL, 1990; JIMÉNEZ *et al.*, 1999) and Atlas (SADKI, 1996).

#### IV. DISCUSSION AND CONCLUSIONS

Three species of *Hebetoxyites* occur in the lower Bajocian, Ovale and Laeviuscula zones of the Iberian Range: *H. hebes* BUCKMAN, *H. incongruens* BUCKMAN and *H. mouterdei* FERNÁNDEZ-LÓPEZ. Both dimorphs, macroconchs and microconchs, occur as taphonic populations of type-2, with dominant pre-adults, due to autochthonous biogenic production of shells by miodemic (actively biodispersed) or parademic (passively biodispersed) populations on the Iberian platform system. The occurrence of indigenous populations of these western Tethyan species of *Hebetoxyites* inhabiting shallow-water marine environments indicates immigration and colonization by Submediterranean taxa. This episode of immigration and colonization corresponds with an incipient-deepening phase within a deepening half-cycle of third order, in the Castilian Platform during the early Bajocian. Therefore, in accordance with the terminology presented by WESTERMANN (2001), two regional bio-events controlled by changes of relative sea level can be distinguished: 1) regional appearance and immigration of *Hebetoxyites* at the Discites/Ovale transition and 2) regional disappearance of the representatives of *Hebetoxyites* at the Laeviuscula/Sauzei transition.

In conclusion, a chronocline can be recognized, beginning with stout forms of the Ovale Zone, strongly ribbed with simple falcoid ribs, narrow umbilicus and raised umbilical margin (including *H. mouterdei*) through intermediate form like *H. hebes*, the type of the genus, to oxycones of the Laeviuscula Zone with blunt, simple or irregularly branched ribbing, numerous secondaries on the outer flank and minute umbilicus with a distinct margin (including *H. incongruens*). This chronocline represents a peramorphic outcome of palingenetic evolution and provides a basis for biochronology, subzonal division and correlation within the Ovale and Laeviuscula zones in the Iberian Range (Fig. 9). The lineage origination of *Hebetoxyites* remains unresolved, but Hebetoxyitidae evolved in addition to the parallel phyletic groups of Haplocerina, Lissoceratidae and Oppeliidae, during the late Aalenian and early Bajocian.

Ovale Zone	Laeviuscula Zone
	<i>Hebetoxyites hebes</i> Buckman [M+m]
	<i>Hebetoxyites incongruens</i> Buckman [M+m]
	<i>Hebetoxyites mouterdei</i> Fernandez-Lopez [M+m]

Fig. 9: Range chart of the three species of *Hebetoxyites* identified in the Iberian Range from the lower Bajocian, Ovale and Laeviuscula zones.

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## Appendix

Abbreviations and measurements for specimens of *Hebetoxyites* from the Iberian Range. Stratigraphical information is indicated by a locality number and section letter: sections 1MT (Masada Toyuela), 1GA and 2GA (Gea de Albarracin), 36L (Llaberia km 36-Bco. Romulta), M (Moscardon), ON (Obon Norte) and VE (Villel); stratigraphical levels and /n = number of specimen. [M] and [m] indicate macroconch and microconch respectively. Measurements are given in mm and include maximum shell diameter at which the following measurements were taken (D), whorl-height (H), whorl-height/diameter ratio (H/D), whorl-width (W), whorl-width/diameter ratio (W/D), umbilical diameter (U), umbilicus/diameter ratio (U/D), whorl-width/whorl-height ratio (W/H) and external ribs per half whorl (Ne/2).

Table 1: Measurements for the specimens of *Hebetoxyites hebes* BUCKMAN, 1924 [M & m].

Specimen	Figure		D	H	H/D	W	W/D	U	U/D	W/H	Ne/2
1MT2/1	5B	[M]	59.0	34.0	57.6%	13.0	22.0%	4.3	7.3%	0.38	28
			37.0	22.0	59.5%	9.0	24.3%	4.4	11.9%	0.41	–
1MT2/358	5E	[M]	43.0	23.8	55.3%	8.5	19.7%	3.1	7.3%	0.36	26
1MT2/326	5F	[M]	41.0	24.6	60.0%	7.8	19.1%	3.0	7.3%	0.32	20
1MT2/325	4A, 5H	[M]	39.0	22.7	58.2%	8.7	22.4%	3.7	9.4%	0.38	25
1MT2/7	–	[M]	35.0	19.0	54.3%	8.2	23.4%	5.0	14.3%	0.43	27
1GA39/1	–	[M]	32.0	17.4	54.4%	6.5	20.3%	4.9	15.3%	0.37	25
1MT2/9	–	[M]	32.0	18.6	58.1%	7.5	23.4%	4.0	12.5%	0.40	26
1MT2/333	–	[M]	31.0	14.3	46.1%	7.7	24.8%	4.1	13.2%	0.54	20
1MT2/354	5J	[M]	26.0	14.0	53.8%	6.1	23.5%	2.8	10.8%	0.44	20
1MT2/369	5M	[m]	26.0	11.0	42.3%	4.7	18.1%	5.3	20.4%	0.43	22
1MT2/367	5P	[m]	26.0	10.2	39.2%	5.9	22.7%	6.6	25.4%	0.58	17
2GA21/2	5K	[M]	25.0	13.4	53.6%	4.9	19.6%	3.8	15.2%	0.37	21
			20.0	11.0	55.0%	4.1	20.5%	3.7	18.5%	0.37	20
1MT2/370	5N	[m]	25.0	10.7	42.8%	5.0	19.8%	7.1	28.4%	0.46	18
1MT2d/1206	4B,5Q	[m]	25.0	10.4	41.6%	4.0	16.0%	7.1	28.4%	0.38	20
1MT2/372	5O	[m]	24.6	9.8	39.6%	5.1	20.7%	6.4	26.0%	0.52	18
1MT2/353	4C, 5L	[M]	20.0	10.2	51.0%	4.6	23.0%	3.3	16.5%	0.45	13
1MT2/331	5I	[M]	20.0	10.2	51.0%	4.6	23.0%	4.1	20.5%	0.45	17

Table 2: Measurements for the specimens of *Hebetoxyites incongruens* BUCKMAN, 1924 [M & m].

Specimen	Figure		D	H	H/D	W	W/D	U	U/D	W/H	Ne/2
1MT2/328	–	[M]	62.0	36.7	59.2%	12.5	20.2%	3.5	5.6%	0.34	26
1MT2d/1212	6D	[M]	57.0	34.0	59.6%	12.8	22.5%	3.1	5.4%	0.38	35
1MT2/2	6E	[M]	52.3	30.9	59.1%	10.4	19.9%	3.3	6.3%	0.34	29
1MT2/8	–	[M]	35.0	19.0	54.3%	7.3	20.9%	3.0	8.6%	0.38	23
			23.4	12.3	52.6%	5.3	22.6%	3.0	12.8%	0.43	–
1MT2d/1204	6G	[m]	32.0	13.5	42.2%	5.9	5.0%	6.9	21.6%	0.44	29
1MT2/368	6H	[m]	31.5	13.9	44.1%	6.1	19.4%	6.5	20.6%	0.44	23
1MT2/365	4D, 6J	[m]	26.0	11.1	42.7%	4.6	17.7%	6.4	24.6%	0.41	26

Table 3: Measurements for the specimens of *Hebetoxyites mousterdei* FERNÁNDEZ-LOPEZ, 1985 [M & m].

Specimen	Figure		D	H	H/D	W	W/D	U	U/D	W/H	Ne/2
1MT2/4	7B	[M]	52.0	28.5	54.8%	10.3	19.8%	4.4	8.5%	0.36	21
1MT2/310	7A	[M]	51.0	30.0	58.8%	12.0	23.5%	4.5	8.8%	0.40	18
1MT2/5	7C	[M]	45.0	24.9	55.3%	9.9	22.0%	6.7	14.9%	0.40	17
1MT2/312	7D	[M]	36.0	19.5	54.2%	9.4	26.1%	4.6	12.8%	0.48	18
1MT2/301	7G	[M]	35.0	17.7	50.6%	8.8	25.1%	4.4	12.6%	0.50	19
1MT2/1211	7F	[M]	34.0	18.3	53.8%	9.4	27.6%	4.6	13.5%	0.51	17
			24.0	13.0	54.2%	7.2	30.0%	4.6	19.2%	0.55	16
1MT2/1049	7H	[M]	31.0	16.0	51.6%	6.7	21.6%	4.2	13.5%	0.42	–
1MT2/1069	7K	[M]	25.0	12.9	51.6%	5.6	22.4%	4.3	17.2%	0.43	15
ON17/1 holotype	4F, 7L	[m]	24.0	11.0	45.8%	6.1	25.4%	6.8	28.3%	0.55	17
			15.0	6.5	43.3%	4.2	28.0%	4.0	26.7%	0.65	16
1MT2/308	7J	[M]	23.0	11.4	49.6%	6.0	26.1%	5.1	22.2%	0.53	15
1MT2/307	–	[M]	15.0	6.8	45.3%	3.6	24.0%	4.3	28.7%	0.53	16